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Functional diversity in an Amazonian rainforest of French Guyana: a dual isotope approach ($\delta^{15}N$ and $\delta^{13}C$)

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Abstract Functional aspects of biodiversity were investigated in a lowland tropical rainforest in French Guyana (5°2′N, annual precipitation 2200 mm). We assessed leaf $\delta^{15}N$ as a presumptive indicator of symbiotic N_2 fixation, and leaf and wood cellulose $\delta^{13}C$ as an indicator of leaf intrinsic water-use efficiency (CO_2 assimilation rate/leaf conductance for water vapour) in dominant trees of 21 species selected for their representativeness in the forest cover, their ecological strategy (pioneers or late successional stage species, shade tolerance) or their potential ability for N_2 fixation. Similar measurements were made in trees of native species growing in a nearby plantation after severe perturbation (clear cutting, mechanical soil disturbance). Bulk soil $\delta^{15}N$ was spatially quite uniform in the forest (range 3–5‰), whereas average leaf $\delta^{15}N$ ranged from −0.3‰ to 3.5‰ in the different species. Three species only, *Diplotropis purpurea*, *Recordoxylon speciosum* (Fabaceae), and *Sclerolobium melinonii* (Caesalpiniaceae), had root bacterial nodules, which was also associated with leaf N concentrations higher than 20 mg g^{-1}. Although nodulated trees displayed significantly lower leaf $\delta^{15}N$ values than non-nodulated trees, leaf $\delta^{15}N$ did not prove a straightforward indicator of symbiotic fixation, since there was a clear overlap of $\delta^{15}N$ values for nodulated and non-nodulated species at the lower end of the $\delta^{15}N$ range. Perturbation did not markedly affect the difference $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$, and thus the isotopic data provide no evidence of an alteration in the different N acquisition patterns. Extremely large interspecific differences in sunlit leaf $\delta^{13}C$ were observed in the forest (average values from −31.4 to −26.7‰), corresponding to intrinsic water-use efficiencies (ratio CO_2 assimilation rate/leaf conductance for water vapour) varying over a threefold range. Wood cellulose $\delta^{13}C$ was positively related to total leaf $\delta^{13}C$, the former values being 2–3‰ higher than the latter ones. Leaf $\delta^{13}C$ was not related to leaf $\delta^{15}N$ at either intraspecific or interspecific levels. $\delta^{13}C$ of sunlit leaves was highest in shade hemitolerant emergent species and was lower in heliophilic, but also in shade-tolerant species. For a given species, leaf $\delta^{13}C$ did not differ between the pristine forest and the disturbed plantation conditions. Our results are not in accord with the concept of existence of functional types of species characterized by common suites of traits underlying niche differentiation; rather, they support the hypothesis that each trait leads to a separate grouping of species.

Key words Tropical rainforest · Stable isotopes · Interspecific diversity · Root symbioses · Functional grouping

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Introduction

Pristine neotropical rainforests on crystalline rocks are characterized by a limited stock of mineral nutrients because of acid unsaturated soils, intense drainage and rapid decomposition of soil organic matter. The

consequence is that most nutrients are stored in the biomass itself and their turnover is very fast. Moreover, growing interest in the sustainable management of this type of forest leads to a new concern: how to maintain the stability of the equilibrium while exporting part of the wood biomass and the nutrients it contains? The replenishment of the stock essentially depends on the ability of the trees to acquire nutrients before they are leached. The role of nitrogen is essential in this respect because of its major contribution to biomass accumulation and its capacity for leaching. The symbiotic fixation of atmospheric N_2 by nodulated legume species is therefore a crucial process, possibly compensating for N losses at the ecosystem level (Pate et al. 1993).

There is little detailed information on the contribution of nitrogen-fixing trees to the nitrogen cycle in primary neotropical rainforests. Of over 19,000 indexed species of tropical Leguminosae only 20% have been examined for bacterial nodulation (Allen and Allen 1981; Faria et al. 1984; Souza-Moreira et al. 1992) and their relative importance in canopies is poorly documented.

As suggested by Delwiche et al. (1979), the natural isotopic composition of plant tissues may constitute a presumptive indicator of nitrogen fixation to be used for spotting nitrogen-fixing plants in unexplored ecosystems (Virginia et al. 1982). The ^{15}N abundance of atmospheric dinitrogen is invariant (Mariotti 1984) and is used as a standard reference value ($\delta^{15}N = 0‰$). The $\delta^{15}N$ of biologically fixed nitrogen ranges between $-2‰$ and $0‰$ (Yoneyama et al. 1986; Kurdali et al. 1993), while that of the soil ranges between -10 and $+20‰$ depending on the type of ecosystem (Feigin et al. 1974). Non-fixing plants, that use only soil nitrogen, reflect the $\delta^{15}N$ of the soil N sources; fixing plants, using both atmospheric and soil N, present intermediate values. Whenever the $\delta^{15}N$ value of a tree is close to that of fixed N, but different from that of neighbouring trees known to be non-fixing, this may suggest that the former tree is highly dependent on fixation for its N supply (Kurdali et al. 1993). However, low $\delta^{15}N$ values in the tree tissues may also be due to the heterogenous distribution of $\delta^{15}N$ in the soil, to different abilities of roots and mycorrhizal fungi to use various pools of soil N with different ^{15}N abundances (Handley et al. 1993; Högberg 1990), or to the existence of specific N isotope discrimination effects related to different metabolic pathways (Bergersen et al. 1988; Handley and Raven 1992; Pate 1994). Therefore, $\delta^{15}N$ can only be considered as an indirect index of the various N acquisition and utilisation specialisations existing in natural ecosystems (Handley and Scrimgeour 1997; Högberg 1997). The putative N_2-fixing status of a tree species detected using the $\delta^{15}N$ approach has to be checked by conventional methods such as the observation of bacterial symbioses or the assessment of acetylene reduction activity (ARA, Balandreau 1976).

Besides the variability in $\delta^{15}N$, natural forest ecosystems are also characterized by important interspecific and intraspecific differences in $\delta^{13}C$ of plant material (Körner et al. 1991; Balesdent et al. 1993; Marshall and Zhang 1994; Brooks et al. 1997), essentially reflecting differences in leaf intrinsic water-use efficiency, i.e. the quotient of CO_2 assimilation rate (A) on leaf conductance for water vapour diffusion (g) (Farquhar et al. 1989). The precise nature (genetic or environmental) and the ecological implications of this variability remain unclear (Flanagan et al. 1992; Zhang et al. 1996; Nguyen-Queyrens et al. 1998). There have been attempts to relate interspecific and inter-site variations in $\delta^{13}C$ to those in $\delta^{15}N$ in dry tropical conditions (Schulze et al. 1991, Handley et al. 1994). Underlying mechanisms may involve the dependence of both A and g on leaf N concentration (Field and Mooney 1986; Guehl et al. 1995) which in turn is dependent on the type of N acquisition and utilisation and thus possibly on $\delta^{15}N$ (Knight et al. 1993; Kumarasinghe et al. 1992).

Despite the ecological interest of tropical rainforests, and their high species diversity, no study on the diversity in $\delta^{15}N$ or $\delta^{13}C$ and on the relationships between these variables has been carried out in these ecosystems to our knowledge. We used such an approach in a lowland primary rainforest of French Guyana with the following objectives:

1. To assess the site variability of $\delta^{15}N$ and $\delta^{13}C$ in the litter and the soil, which is a prerequisite for investigations of the N acquisition types of trees based on leaf $\delta^{15}N$ values. Comparing $\delta^{15}N$ and $\delta^{13}C$ values among leaves, litter and soil may also reveal specific traits of the overall N and C cycling at the ecosystem level (Högberg 1997).
2. To assess the interspecific variability of $\delta^{15}N$ and to determine if these values can be used as an indication of symbiotic N_2 fixation.
3. To assess the interspecific variability of $\delta^{13}C$ and the relationships between $\delta^{13}C$ on the one hand, and $\delta^{15}N$ and/or other plant traits on the other hand. Ultimately, is it possible to define an effective (i.e. unique and simple; Grime 1977; Tilman 1988; Chapin 1997) grouping of species emcompassing the different plant-environment interactions reflected by the dual $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures? Such a grouping would be of paramount interest for the modelling and simulation of ecosystem function.

Species were selected as representative of the pristine forest cover, of the different light adaptation strategies and for their potential ability to fix dinitrogen (legume families). Measurements were also made in trees of native species growing in a nearby 10-year-old plantation which was installed after severe anthropogenic perturbation (clear cutting, mechanical soil disturbance). Under these conditions both the N availability in the soil and the root symbiotic status of the trees were likely to be altered, possibly affecting the C and N isotopic signatures.

Materials and methods

Sampling sites

The study area is in the northern part of French Guyana, in the experimental forest zone of Paracou (CIRAD-Forêt) described by Bariteau and Geoffroy (1989), located between Kourou and Sinnamary, about 80 km west of Cayenne near the Atlantic coast (5°20′N, 52°50′W, 40 m asl). The soils are oxisoils (*Keys to Soil Taxonomy*, Cornell University, 1985, Ithaca NY, USA) developed on migmatite and shales. The dense primary forest (projected LAI = 8; personal communication André Granier) has a basal area of about 35 m^2 ha^{-1}. Three angiosperm families (out of a total of 73) represent 60% of the rainforest in the study area: the *Lecythidaceae* (genera *Eschweilera* and *Lecytis*), the *Caesalpiniaceae* (genera *Eperua* and *Dicorynia*) and the *Chrysobalanaceae* (genera *Licania* and *Parinari*) (Favrichon 1994). The climate is characterized by a distinct seasonal pattern: a wet season from December to August, which is normally interrupted in February or March by a short dry period, and a long dry season from September to November with monthly precipitation of less than 100 mm. Average annual precipitation is 2200 mm. Mean temperature is 25°C with low seasonal changes (Huc et al. 1994).

The trees sampled were chosen either in the primary rainforest or in a nearby 10-year-old plantation of local native species (Huc et al. 1994). Table 1 lists the 21 tree species studied, belonging to 15 families, and indicates the sampling design. The species were chosen according to three criteria: (1) relative abundance in the type of forest studied, (2) possibility of comparing the results in the forest and in the plantation, and (3) consideration of a wide range of taxa. In Table 1 we have also indicated the light adaptation features of the different species as defined by Favrichon (1994), who established a functional grouping of species based on growth dynamics observations made on established trees either in the pristine cover or in response to microclimatic changes induced by thinning of various intensities. The species investigated in the present study fell within three groups : (1) shade-tolerant species that could poten-

Table 1 Root characteristics and light requirements (functional groups defined by Favrichon 1994) of the different species. All species were endomycorrhizal with no ectomycorrhizas. The representativity of the species (proportion of the total stand basal area of the forest) and the number of trees sampled in the forest and the plantation has also been reported. The total stand basal area of the forest was 31.4 m^2 ha^{-1}; the species investigated represented 39.2% of this value. Letter *p* refers to long-lived heliophilic pioneer or gap species

Species	Roots and root symbioses				Light adaptation features (shade tolerance)	% Stand basal area	Number of trees	
	Fine root diameter (mm)	Branching density	Peritrophic associations	Bacterial nodules			Forest	Plantation
Caesalpiniaceae								
Dicorynia guianensis Amshoff	0.15	High	Abundant	None	Hemitolerant	2.2	11	4
Eperua falcata Aublet	0.60	Low	Abundant	None	Hemitolerant	7.6	4	4
Peltogyne venosa Benth.	0.20	High	Abundant	None	Hemitolerant	0.1	1[a]	4[a]
Recordoxylon speciosum Norm	0.20	High	None	Abundant	Hemitolerant	0.9	1[b]	0
Sclerolobium melinonii Harms	0.30	High	Abundant	Abundant	Heliophilic (p)	0.8	4	0
Fabaceae								
Diplotropis purpurea Amshoff	0.20	Medium	None	Abundant	Heliophilic	0.2	2	4
Mimosaceae								
Parkia nitida Miquel	0.30	Low	None	None	Heliophilic	0.6	2[a]	0
Bignognaceae								
Jacaranda copaia D. Don	0.40	Low	None	None	Heliophilic (p)	0.3	0	4[a]
Caryocaraceae								
Caryocar glabrum Pers.	nd	nd	nd	nd	Hemitolerant	0.9	0	4[a]
Chrysobalanaceae								
Licania sp.	0.30	Low	None	None	Tolerant	4.7	1[a]	0
Parinari sp.	0.15	High	None	None	nd	0.4	1[a]	0
Clusiaceae								
Platonia insignis Mart.	0.30	Low	None	None	Hemitolerant	0.3	1[b]	4[b]
Goupiaceae								
Goupia glabra Aublet	0.20	High	None	None	Heliophilic (p)	1.1	3	4
Lecytidaceae								
Eschweilera odora Miers	0.20	Low	None	None	Tolerant	9.1	6[a]	0
Meliaceae								
Carapa guianensis Aublet	0.40	Low	None	None	Heliophilic (p)	0.9	3	4
Myristicaceae								
Virola michelii Heckel	0.10	High	None	None	Heliophilic	0.3	3[a]	0
Myrtaceae								
Eugenia sp.	0.40	High	None	None	Tolerant	0.1	1[a]	0
Sapotaceae								
Pradosia cochleria Pen.	nd	nd	nd	nd	Tolerant	4.2	1[a]	0
Micropholis guianensis DC.	0.40	High	None	None	Tolerant	1.2	1[a]	0
Sterculiaceae								
Sterculia excelsa Mart.	0.30	High	None	None	Heliophilic (p)	1.0	1[a]	4[a]
Vochysiaceae								
Qualea rosea Aublet	0.15	Low	None	None	Hemitolerant	2.3	1[a]	0

nd, not determined
[a] No soil sampling
[b] No soil and wood sampling

tially reach the upper canopy layer, (2) shade hemitolerant and emergent species, (3) heliophilic species. Within the latter group it is possible to distinguish two sub-groups based on forest regeneration features (Prevost 1981; Riéra et al. 1990): long-lived heliophilic pioneer or gap species which are able to colonize openings or large gaps in the forest, and heliophilic non-pioneer species for which development is not associated with wide openings.

Nineteen and ten species were sampled in the pristine forest and in the plantation, respectively. Eight species were represented in both situations.

In the primary forest cover of the study area, leaf $\delta^{13}C$ was shown to be strongly dependent on the leaf position and the light conditions (Buchmann et al. 1997a). Therefore, one might expect understorey or suppressed trees to exhibit more negative $\delta^{13}C$ values than dominant or co-dominant trees. In a preliminary study, we assessed this effect by measuring the $\delta^{13}C$ of wood cellulose (see Sampling procedures, below) of trees of two major species (*Eperua falcata* and *Dicorynia guianensis*) covering a wide range of diameter at breast height (DBH). In both species the $\delta^{13}C$ values for DBH < 30 cm were clearly lower than for DBH above this threshold (Fig. 1). In this latter group of trees no significant correlation between DBH and $\delta^{13}C$ was observed. Thus, only trees with DBH $\geq$ 30 cm were considered in the pristine forest.

In the primary forest, nine species with at least two tree replicates were in the same 6.25 ha square plot. *Dicorynia guianensis* and *Eschweilera odora*, two abundant species in the study area, were represented by 11 and 6 trees, respectively. These trees were roughly scattered along a diagonal of the plot, which also corresponded to a top- to down-hill toposequence (elevation difference 15 m). No significant spatial patterns in isotopic signatures were observed in either species according to this gradient (data not shown). Thus, spatial coordinates of trees were not considered as a source of variation for $\delta^{15}N$ and $\delta^{13}C$. Other species, represented by single trees, were sampled near the plot.

The plantation consisted of 20×20 m monospecific elementary plots; tree spacing was 3 m $\times$ 3 m. Trees were chosen at random inside the plots but no measurements were made on border trees. Differences in the competitive status among trees were less pronounced than in the forest; the DBH of the selected trees ranged from 6 cm to 25 cm.

Sampling procedures and sample processing

All sampling took place in dry seasons. Leaf and wood samples were taken for all species in March 1993. Litter and soil samples were taken in September 1994 in six species (*Carapa guianensis*, *Dicorynia guianensis*, *Diplotropis purpurea*, *Eperua falcata*, *Goupia glabra*, *Sclerolobium melinonii*) selected for their differing symbiotic status and their contrasting leaf $\delta^{15}N$ values. All these species but *Sclerolobium melinonii* (forest only) were represented both in the forest and in the plantation.

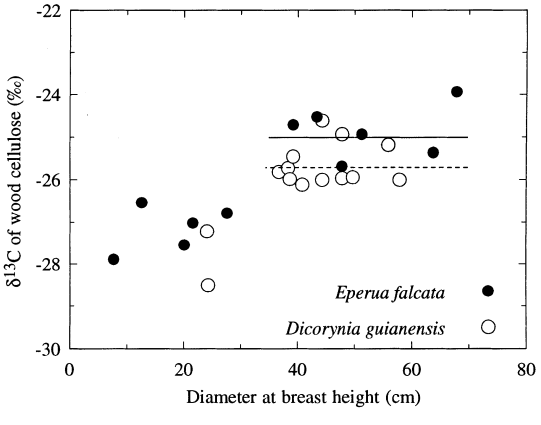


Fig. 1 Relationship between carbon isotope composition ($\delta^{13}C$) of wood cellulose and stem diameter at breast height (DBH) in *Eperua falcata* and *Dicorynia guianensis* trees from the experimental area. Isotopic measurements were made using *c.* 5-cm-long wood cores taken at breast height. *Horizontal lines* represent the average $\delta^{13}C$ values for both species for those trees with DBH > 30 cm

Healthy, fully expanded leaves from the upper canopy layer were collected from small branches shot down from the top of trees. Thick woody petioles and the rachis of composite leaves were removed and the surface area of fresh leaves or folioles was determined by image analysis. They were oven-dried at 65°C overnight at the end of the collecting day and weighed for calculating leaf mass per unit area (LMA = dry weight/projected leaf area). The leaves were then finely ground and the powdered material was packed in air-tight containers. One wood core (5 mm diameter and approximately 5 cm long) was taken at breast height from each tree using a Pressler borer. These wood samples were oven-dried at 65°C overnight.

Litter and soil samples were taken under trees belonging to six different species both in the forest and in the plantation (Table 1). Litter (intact, fragmented or decomposing dead leaves) and soil (0–10 cm deep, mineral soil) were collected in four vegetation-free 0.25-m^2 square plots in four directions at a distance of approximately 1 m from the basis of the trees. The four litter or soil samples per tree were pooled and homogenized by thoroughly mixing, and a subsample of *ca.* 0.5 l (soil) or 2 l (litter) was kept for further processing. Soil and litter subsamples were oven-dried at 65°C overnight. Litter was ground and packed as for leaves. Roots and large organic debris were removed from the dried soil samples which were first crushed and sieved through a 2-mm mesh, then finely ground in a ring grinder before packing in air-tight containers.

Roots and symbiotic associations

Fine roots in the 0–10 cm soil layer were collected from each sample tree by tracing thick roots from the base of the trunk to their ultimate branchings; they were immediately put in plastic bags and carried to the laboratory in an ice box. The same day, they were gently washed in running tap water and stored in water at 4°C before observation using a dissecting microscope during the following days. The following features were noted: branching pattern, diameter of the thinnest roots, ectomycorrhizas, peritrophic associations (short roots with a fungal sheath but no Hartig net) and bacterial nodules. The presence/absence of a Hartig net was ascertained by hand-cutting putative ectomycorrhizas and observing the sections with a microscope. The root samples were then cleared with KOH and H_2O_2 and stained with acid fuchsin for the observation of endomycorrhizas using the microscope; inter- and intracellular hyphae, arbuscules, coils and vesicles were noted (Philips and Hayman 1970).

Elemental and isotopic analyses

Nitrogen and carbon concentrations, as well as the $\delta^{13}C$ and $\delta^{15}N$ values of the samples, were measured using a custom-made elemental analyser (Service Central d'Analyses, CNRS, Vernaison, France) coupled with a DELTA S isotopic ratio mass spectrometer (Finnigan Mat, Bremen, Germany). Two separate subsamples (about 100 µg N or C) of the powdered material (leaf, litter or soil) were used for (1) C concentration and $\delta^{13}C$ and (2) N concentration and $\delta^{15}N$ determinations.

The bark was discarded from the cores. Wood cellulose was purified according to the method described by Deleens (1980). For each sample, 15 mg of cellulose was weighed and combusted in quartz vessels in pure O_2. The carbon was thus completely converted into CO_2 which was used for carbon isotopic measurements.

Leaf cellulose $\delta^{13}C$ was determined according to the same procedure as for wood in six species (*Carapa guianensis*, *Eperua*

falcata, *Goupia glabra*, *Parkia nitida*, *Sclerolobium melinonii*, *Virola michelii*) selected for their contrasting bulk leaf $\delta^{13}C$ values.

Relative abundances of ^{13}C and ^{15}N were expressed in terms of the conventional $\delta‰$ notation, according to the relation:

$$\delta‰ = \frac{R_{sample} - R_{standard}}{R_{standard}} 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ refer to the $^{13}C/^{12}C$ or ^{15}N /^{14}N molar ratio in the sample and the Pee Dee Belemnite (C) or atmospheric N_2 (N) standards, respectively. Precision of measures was 0.2‰.

Phosphorus was analysed by ICP-AES (ARL 3580 instrument) on line 178.2 nm. A 200-mg sample was burned at 450 °C in a platinium vessel. Ashes were treated with perchloric, nitric and fluoridric acids to dryness, the residue was dissolved with nitric acid. The accuracy of measurements is estimated to be between 2 and 5%.

Statistical analysis

Conventional statistical analyses (correlations, linear regressions, anova) were performed using the Statview Macintosh Software. For the classification of species according to both leaf and wood cellulose $\delta^{13}C$ values (couples of values considered simultaneously) in the forest situation, a cluster analysis was performed (Ward's minimum minimum variance method) by using SAS/STAT software (SAS Institute 1988). The optimal number of clusters was taken as the one for which the ratio of the variances within cluster/between cluster levels was minimized.

Results

Fine root morphology and symbiotic status

The different species displayed a high diversity in branching density and diameter of fine roots (from 0.1 to 0.6 mm) (Table 1). On average, the thickest roots were also the less branched.

All the studied trees were endomycorrhizal, with no ectomycorrhizas. However, four species in the family Caesalpiniaceae (*Dicorynia guianensis*, *Peltogyne venosa*, *Sclerolobium melilonii* and *Eperua falcata*) had peritrophic associations (i.e. a fungal mantle but no Hartig net) in addition to the endomycorrhizae. The endomycorrhizas were all of the vesicular-arbuscular type due to Zygomycetes fungi (Glomales), with abundant intra- and inter-cellular vesicles and mycelium and external, thick, non-septate hyphae with terminally-attached large spores of various shapes. However, typical arbuscules were extremely rare and replaced by intracellular hyphal coils.

Abundant bacterial nodules (lobed, 10–30 mm) were observed in *Diplotropis purpurea* (Fabaceae). *Sclerolobium melilonii* (Caesalpiniaceae) had abundant bacterial nodules of another type (spherical, 3–5 mm) *Recordoxylon speciosum* presented archaic nodules (i.e. bacteroids not released in the cell cytoplasm, Faria et al. 1984). The diversity of root morphology and types of symbioses found in the sample was consistent with the results of Béreau and Garbaye (1994) where more detailed descriptions are given.

Leaf characteristics and phosphorus concentration

In the forest, leaf thickness and leaf mass per unit projected area (LMA) were lowest in *Sclerolobium melinonii*, *Parkia nitida*, *Eperua falcata* and *Virola michelii*, and were highest in *Carapa guianensis* and *Eschweilera odora* (Table 2). Leaf thickness and LMA were closely related (LMA = 280 × leaf thickness + 70, $r^2 = 0.83$, pooled dataset from the forest and the plantation). Leaf thickness and LMA were generally similar in the forest

Table 2 Leaf characteristics of the different species in the forest and in the plantation. Species were ordered according to their light adaptation features (Favrichon 1994). Letter *p* refers to long-lived heliophilic pioneer or gap species. Missing values correspond to situations in which no measurements were made. For a given species and variable, mean values ± SE followed by different letters are significantly different ($P < 0.05$)

Species	Leaf thickness (mm)		Leaf mass per unit area (g m^{-2})		Leaf P concentration (μg g^{-1})	
	Forest	Plantation	Forest	Plantation	Forest	Plantation
Shade tolerant species						
Eschweilera odora	0.38 ± 0.01	–	184 ± 9	–	472 ± 27	–
Hemitolerant species						
Caryocar glabrum	–	–	–	–	–	747 ± 25
Dicorynia guianensis	0.26 ± 0.01[b]	0.29 ± 0.01[a]	144 ± 4	138 ± 3	597 ± 28	633 ± 35
Eperua falcata	0.18 ± 0.01[a]	0.15 ± 0.01[b]	116 ± 4	106 ± 3	680 ± 21	732 ± 43
Peltogyne venosa	–	0.24 ± 0.02	–	151 ± 11	–	813 ± 35
Platonia insignis	–	–	–	–	–	442 ± 16
Heliophilic species						
Carapa guianensis (p)	0.36 ± 0.05	0.32 ± 0.01	171 ± 9	153 ± 9	670 ± 10[a]	775 ± 20[b]
Diplotropis purpurea	–	0.20 ± 0.01	–	111 ± 5	–	672 ± 14
Goupia glabra (p)	0.19 ± 0.01	0.22 ± 0.01	122 ± 2	138 ± 8	577 ± 14	610 ± 15
Jacaranda copaia (p)	–	0.32 ± 0.01		164 ± 6	–	581 ± 22
Parkia nitida	0.17 ± 0.01	–	136 ± 23	–	665 ± 39	–
Sclerolobium melinonii (p)	0.16 ± 0.01	–	116 ± 9	–	632 ± 16	–
Sterculia excelsa (p)	–	0.23 ± 0.01	–	128 ± 0.07	–	802 ± 34
Virola michelii	0.20 ± 0.01	–	133 ± 12	–	450 ± 74	–

and in the plantation. In the forest, leaf P concentration ranged from 450 μg g^{-1} (*Virola michelii*) to 680 μg g^{-1} (*Eperua falcata*). There was a tendency for leaf P concentrations to be higher in the plantation than in the forest, but the difference was significant for *Carapa guianensis* only (Table 2).

Leaf nitrogen

In the forest, average total leaf N concentrations ranged from 10 to 27 mg g^{-1} in the different species (Fig. 2) and average leaf $\delta^{15}N$ ranged from −0.3 to 3.5‰ with an even distribution of the values between these extremes (Fig. 2). Leaf N concentration was higher in legume than in non-legume species (Table 3) while $\delta^{15}N$ did not differ between these two groups of species. The species (*Diplotropis purpurea*, *Sclerolobium melinonii* and *Recordoxylon speciosum*) with N concentration values above 20 mg g^{-1} (Fig. 3) were the nodulated legume species (Table 1). Leaf $\delta^{15}N$ was significantly lower in the nodulated than in the non-nodulated species (Table 3) and was highest (3.5‰) in the non-fixing legume species *Dicorynia guianensis* (Fig. 2). $\delta^{15}N$ values close to 0‰ were observed in the nodulated species *Diplotropis purpurea* and *Sclerolobium melinonii*, whereas the other nodulated legume species, *Recordoxylon speciosum*, displayed a clearly positive (2.3‰) value. Furthermore, *Goupia glabra*, a non-nodulated species, displayed $\delta^{15}N$ values close to 0‰ and 8 further species (see Fig. 2) had $\delta^{15}N$ values lower than the one observed for *Recordoxylon speciosum*, leading to an overlap of the $\delta^{15}N$ values between nodulated and non-nodulated species.

The species which were sampled both in the forest and in the plantation displayed either similar leaf N concentrations in the two situations, or higher values in the plantation (*Platonia insignis* and *Carapa guianensis*) (Fig. 2). In contrast, leaf $\delta^{15}N$ was markedly higher in the plantation (values between 1.2 and 3.3‰) than in the forest, except for *Dicorynia guianensis* for which no significant difference was observed between the forest and the plantation.

Site variability of nitrogen and carbon in litter and soil

Total N concentrations of the litter and the soil were less variable than–and poorly (litter) or not (soil) correlated with–that in the leaves, both in the forest and in the

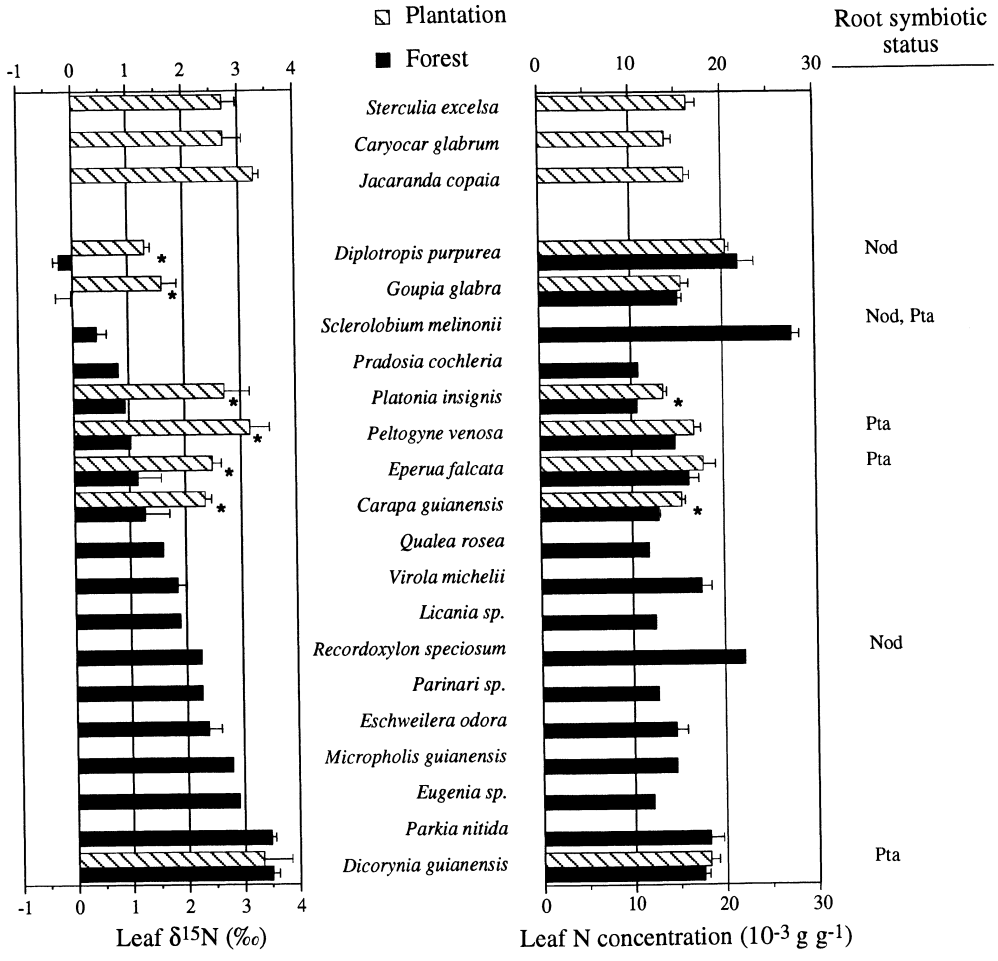


Fig. 2 Nitrogen isotope composition ($\delta^{15}N$) and N concentration in full sunlit leaves of a range of species growing in the forest (dominant or co-dominant trees) and in a nearby 10-year-old plantation with monospecific plots. The species were ordered according to the $\delta^{15}N$ values (average species values ± SE) observed in the forest. The presence of bacterial nodules on roots is indicated by the symbol *Nod*, the presence of peritrophic associations is denoted by the symbol *Pta*. All species were endomycorrhizal with no ectomycorrhizas. For those species occurring in the forest and in the plantation, asterisks denote significant differences between the forest and the plantation (one-way ANOVA, $P < 0.05$)

Table 3 Significance levels (probabilities) from factorial analysis of variance of leaf $\delta^{15}C$, leaf N concentration, leaf $\delta^{13}C$ and wood $\delta^{13}C$ among the 18 different species, the legumineous or non legumineous nature of the species, the nodulated or non nodulated status of trees (see Table 1) and three groups of shade tolerance (tolerant, hemitolerant and heliophilic; after Favrichon (1994), see Table 1 and Fig. 6). Analysis performed in the pristine forest only

Source of variation	Leaf $\delta^{15}N$	Leaf N concentration	Leaf $\delta^{13}C$	Wood $\delta^{13}N$
Species	0.0001	0.0001	0.0001	0.0001
Legume species	0.1679	0.0001	0.0001	0.0025
Nodulation	0.0012	0.0001	0.2470	0.2121
Shade tolerance	0.0009	0.0033	0.0001	0.0168

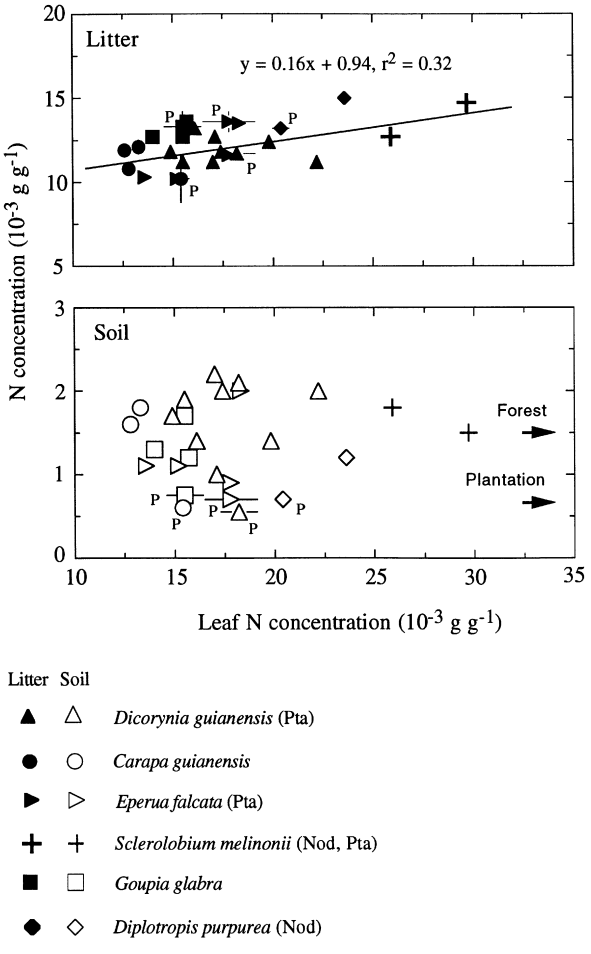


Fig. 3 Relationship between litter or surface mineral soil (0–10 cm depth) N concentration and sunlit leaf N concentration for trees of different species growing in the forest (dominant or co-dominant trees) and in a nearby 10-year-old plantation with monospecific plots. Litter and soil samples were taken under those trees from which leaf samples were taken. Data points represent individual trees in the forest and mean species values (± SE) in the plantation (data points with symbol *P*). *Arrows* in the *lower panel* correspond to the mean values of soil N concentration in the forest and the plantation. The presence of bacterial nodules on roots is indicated by the symbol *Nod*, the presence of endomycorrhizal peritrophic associations is denoted by the symbol *Pta*

plantation (Fig. 3). Litter N concentrations were similar in the forest and in the plantation, whereas soil N concentrations in the plantation were on average half those observed in the forest (Fig. 3). Soil C concentrations were also lower in the plantation (average value 14.2 mg g^{-1}) than in the forest (33.3 mg g^{-1}) and the soil C/N mass ratio (average value 21.1 ± 1.3) did not differ between the forest and the plantation.

The ranges of $\delta^{15}N$ values observed in the litter (individual values from 0.5 to 3‰) and the soil (3 to 5‰) were narrower than that observed in the leaves (−0.6 to 4.2‰, Fig. 4). Litter $\delta^{15}N$ values were significantly ($P < 0.05$) related with leaf $\delta^{15}N$ (Fig. 4). The slope of the overall (forest and plantation) regression line between these variables was 0.26, but the values observed in the plantation were ordered along the 1:1 line (Fig. 4). Soil $\delta^{15}N$ was on average 3‰ higher than litter $\delta^{15}N$. However, the correlations between litter $\delta^{15}N$ and soil $\delta^{15}N$ were not significant, whether the forest and plantation data were considered separately or pooled. There was no significant correlation between soil $\delta^{15}N$ and leaf $\delta^{15}N$ for the pooled forest and plantation – or for the plantation – data (Fig. 4). In the forest, these two variables were significantly related ($\delta^{15}N_{soil} = 0.133\ \delta^{15}N_{leaf} + 3.86$, $r^2 = 0.27$, $P < 0.05$), the slope of the relationship being clearly lower than unity.

Litter $\delta^{13}C$ values were not significantly correlated with leaf $\delta^{13}C$ (Fig. 4). Soil $\delta^{13}C$ values were on average 1.7‰ higher than litter $\delta^{13}C$ values and presented less scatter. Soil $\delta^{13}C$ values were slightly (slope of regression line = 0.19, $P < 0.05$) related to leaf $\delta^{13}C$, but were not related to litter $\delta^{13}C$.

The soil $\delta^{15}N$ values observed for *Diplotropis purpurea*, *Goupia glabra* and *Eperua falcata* were clearly higher in the plantation than in the forest (Fig. 4). Considering the difference $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ in the forest (Table 4), we obtained the same ranking of species as when considering merely the leaf $\delta^{15}N$ values (Fig. 2). However, in contrast with the results observed for $\delta^{15}N_{leaf}$, in all species but *Carapa guianensis*, $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ did not differ between the forest and the plantation.

Leaf and wood cellulose $\delta^{13}C$

In the forest, the different species spanned a wide range of sunlit leaf $\delta^{13}C$, with average values from −26.7‰ in *Recordoxylon speciosum* to −31.4‰ in *Parkia nitida* (Fig. 5). We examined the correlations, both at the individual level and at the level of average species values, between leaf $\delta^{13}C$ on the one hand and the following different variables: LMA, leaf thickness, leaf N and P

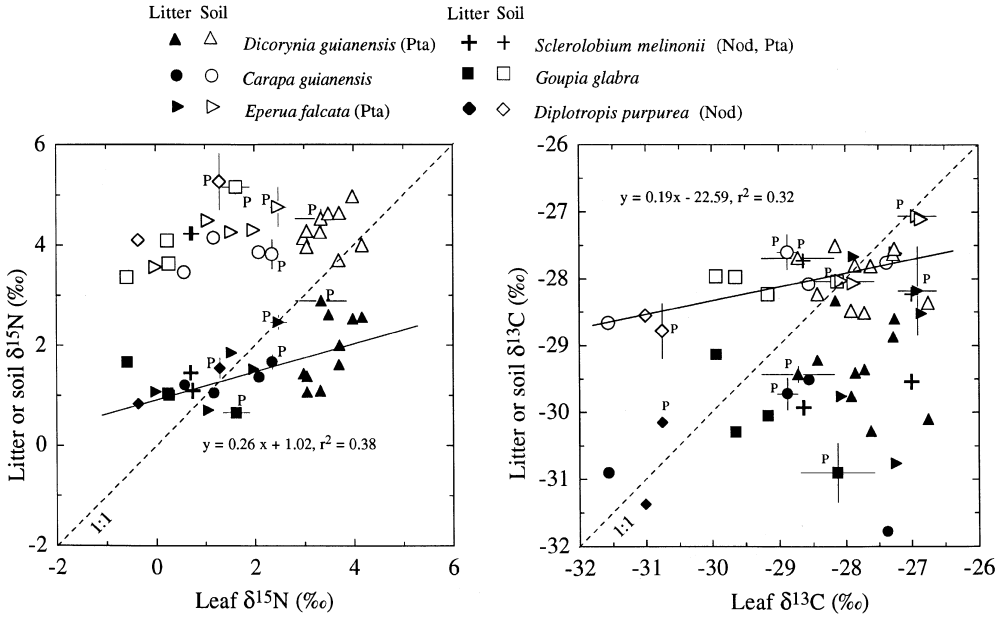


Fig. 4 Relationship between litter or surface soil (0–10 cm depth) $\delta^{15}N$ (or $\delta^{13}C$, right hand side) and bulk sunlit leaf $\delta^{15}N$ (or $\delta^{13}C$) for trees of different species growing in the forest (dominant or co-dominant trees) and in a nearby ten-year-old plantation with monospecific plots. Litter and soil samples were taken under those trees from which leaf samples were taken. Data points represent individual trees in the forest and mean species values (±SE) in the plantation (data points with symbol *P*). The litter $\delta^{15}N$ vs. leaf $\delta^{15}N$ regression line is for the pooled forest and plantation data set. The soil $\delta^{13}C$ vs. leaf $\delta^{13}C$ regression line corresponds to the pooled forest and plantation data set; there was no significant ($P < 0.05$) correlation between litter $\delta^{13}C$ and leaf $\delta^{13}C$. The presence of bacterial nodules on roots is indicated by the symbol *Nod*, the presence of endomycorrhizal peritrophic associations is denoted by the symbol *Pta*

concentrations (per unit leaf mass and per unit leaf area), leaf $\delta^{15}N$. None of these correlations was significant (data not shown).

Wood cellulose and leaf $\delta^{13}C$ values were positively related (Fig. 6), wood cellulose $\delta^{13}C$ values being on average (regression line) 2–3‰ less negative than leaf $\delta^{13}C$ values. Leaf cellulose $\delta^{13}C$ was about 1‰ less negative (regression line) than $\delta^{13}C$ of the bulk leaf material (Fig. 7) and about 2 to 2.5‰ more negative than wood cellulose $\delta^{13}C$. However, in *Carapa guianensis* wood and leaf cellulose $\delta^{13}C$ values were similar.

The cluster analysis, for which we considered couples of values (bulk leaf $\delta^{13}C$, wood cellulose $\delta^{13}C$), led to the distinction of three clusters (Fig. 6). Average leaf $\delta^{13}C$ and $\delta^{13}C$ of wood cellulose values differed by about 4‰ and 2‰ between the two extreme clusters, respectively. Three species (*Sclerolobium melinonii*, *Diplotropis purpurea* and *Eschweilera odora*) were shared between two clusters and one species (*Carapa guianensis*) was shared between the three clusters.

The ranking of the different species for leaf $\delta^{13}C$ in the plantation – as well as the relationship between leaf $\delta^{13}C$ and wood cellulose $\delta^{13}C$ – were similar to the one obtained in the forest (Figs. 5, 6). $\delta^{13}C$ differed significantly between the forest and the plantation only in *Dicorynia guianensis* (lower values in the plantation, Fig. 5).

Discussion

Spatial patterns and overall nitrogen and carbon cycling

In tropical rainforests, a major source of N and C input in soils is the litter material from numerous tree species potentially differing in their leaf N and C concentrations or isotopic compositions (Vitousek et al. 1989; Yoneyama et al. 1993; Huc et al. 1994; Buchmann et al. 1997a; Smith and Read 1997). Thus, in any attempt to assess characteristics of N or C cycling at the ecosystem level, one has to take account of the possible lateral spatial variability of the major variables and processes of the system as it has been shown in tropical (Vitousek et al. 1989) or in temperate (Broadbent et al. 1980; Balesdent et al. 1993) heterospecific forests. In the present study, leaf $\delta^{15}N$ and $\delta^{13}C$ varied widely among tree species, whereas these variables were more uniform in the litter under these trees (Fig. 4). A possible reason for this difference is the lateral dispersal and mixing of the leaves falling from the different tree species with contrasting leaf $\delta^{15}N$ and $\delta^{13}C$.

Soil $\delta^{15}N$ and $\delta^{13}C$ values, which essentially reflect the isotopic signatures of organic pools (Handley and Raven 1992; Boutton 1996), were on average 3‰ ($\delta^{15}N$) and 1.7‰ ($\delta^{13}C$) higher than the corresponding litter values (Fig. 4). Similar patterns have been reported in different types of soils in temperate or tropical forests for $\delta^{15}N$ (Mariotti 1982; Gebauer and Dietrich 1992; Evans and Ehleringer 1994) and for $\delta^{13}C$ (Balesdent et al. 1993; Bird et al. 1996; Martinelli et al. 1996; Buchmann et al. 1997b) and have primarily been attributed to (1) the positive isotopic discrimination occurring during organic matter decomposition processes and humification

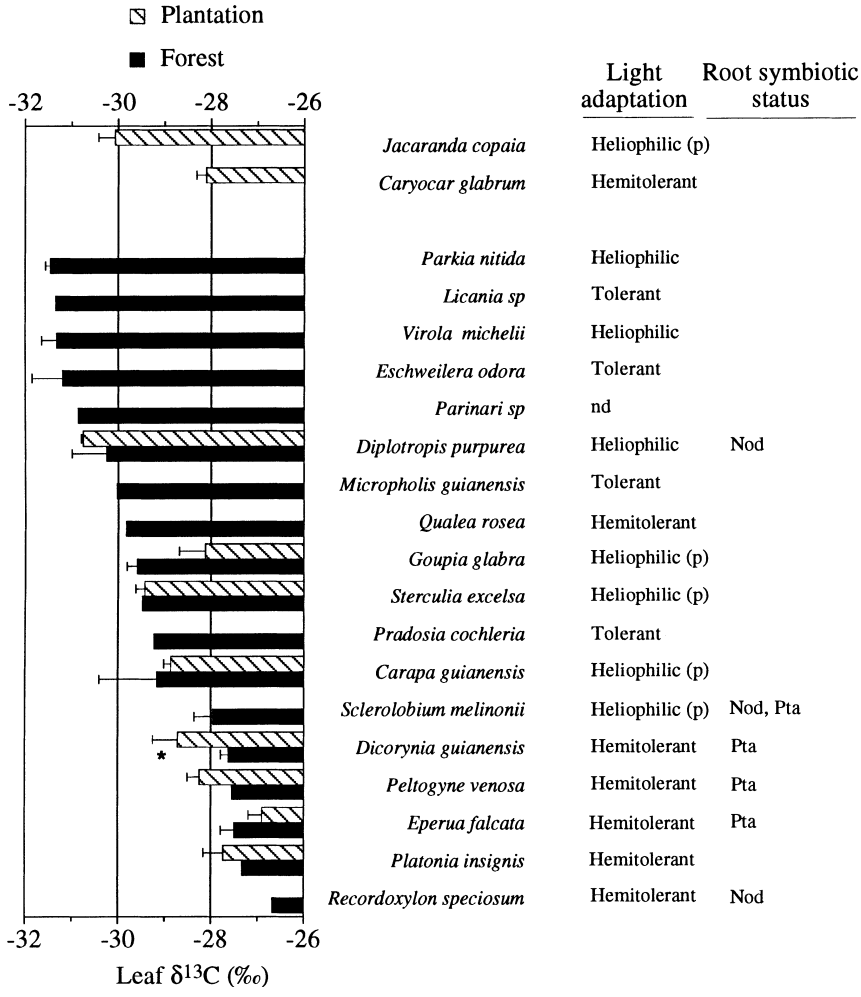
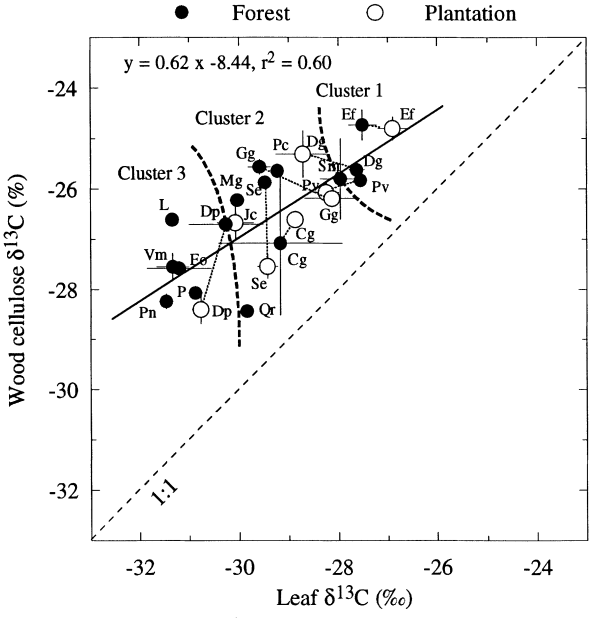


Fig. 5 Carbon isotope composition $\delta^{13}C$ of full sunlit leaves of a range of species growing in the forest (dominant or co-dominant trees) and in a nearby 10-year-old plantation with monospecific plots. The species were ordered according to the $\delta^{13}C$ values (average species values ± SE) observed in the forest. For those species growing in the forest and in the plantation, asterisks denote significant differences between the forest and the plantation (one-way ANOVA, $P < 0.05$). The light adaptation features of the different species are those defined by Favrichon (1994) on the basis of growth observations made on established trees in the pristine cover or in response to microclimatic changes induced by thinnings with various intensities. Letter (*p*) refers to heliophilic pioneer or gap species. The presence of bacterial nodules on roots is indicated by the symbol *Nod*, the presence of peritrophic associations is denoted by the symbol *Pta*

(Mariotti et al. 1981; Balesdent et al. 1993; Evans and Ehleringer 1993) or (2) differential decomposition/preservation kinetics of the different biochemical fractions of organic matter displaying different isotopic compositions (Boutton 1996).

In contrast with the findings of Balesdent et al. (1993) on $\delta^{13}C$ values in a mixed temperate forest, we did not observe any significant correlation between litter and soil $\delta^{13}C$ or $\delta^{15}N$ values when considering spatial variation of these variables (Fig. 4). Due to the non-synchronous leaf fall between species (Lescure et al. 1990) and the high turnover rate of litter which characterize tropical rainforests, litter $\delta^{13}C$ and $\delta^{15}N$ values are likely to display seasonal changes at a given site, whereas the isotopic signatures of soil organic matter, integrating time periods of about five years (Bird et al. 1996), are expected to be more stable over time. It is also noteworthy that the spatial variability of soil $\delta^{13}C$ and $\delta^{15}N$ was low in the highly heterogenous pristine forest we studied, with a maximum range of 1.5‰ between sites for both variables. Using a sampling design similar to the present one, Balesdent et al. (1993) found a range of ca. 4‰ for soil $\delta^{13}C$ between sites in a mixed broad-leaved and coniferous temperate forest.

Soil $\delta^{15}N$ averaged about 4‰ in the forest (Fig. 4). Similar – or even higher – positive values were found in upper soil layers of a series of tropical humid (Yoneyama et al. 1993), subtropical dry (Stock et al. 1995) and temperate cool (Shearer et al. 1978; Mariotti 1982; Nadelhoffer and Fry 1988; Gebauer and Schulze 1991; Gebauer and Dietrich 1993; Yoneyama et al. 1993) forest ecosystems. Interestingly, in spite of similar soil $\delta^{15}N$ values, leaf $\delta^{15}N$ of the trees from the temperate cool conditions were clearly negative in the various species and soil conditions investigated (Mariotti 1982; Gebauer and Dietrich 1993; Gebauer and Schulze 1991) whereas in the warmer types of climate, and particularly in the tropical rainforest we investigated (Figs. 2, 4), trees generally displayed positive – or close to zero – $\delta^{15}N$ values. This opposition may reflect essential differences in nitrogen cycling features between ecosystems (Shearer et al. 1974). Högberg (1990, 1997) proposed that forest ecosystems losing large quantities of nitrogen have high $\delta^{15}N$ values because of ^{15}N enrichment of the residual soil nitrogen sources of trees. Although important nutrient losses through leaching and atmospheric emissions have been suggested for Amazonian forests (Jordan



	Cluster	Light adaptation
Jc, *Jacaranda copaia*	nd	Heliophilic (p)
Pn, *Parkia nitida*	(3)	Heliophilic
L, *licania sp.*	(3)	Tolerant
Vm, *Virola michelii*	(3)	Heliophilic
P, *Parinari sp.*	(3)	nd
Eo, *Eschweilera odora*	(2, 3)	Tolerant
Dp, *Diplotropis purpurea*	(2, 3)	Heliophilic
Mg, *Micropholis guianensis*	(2)	Tolerant
Qr, *Qualea rosea*	(2)	Hemitolerant
Gg, *Goupia glabra*	(2)	Heliophilic (p)
Se, *Sterculia excelsa*	(2)	Heliophilic (p)
Pc, *Pradosia cochleria*	(2)	Tolerant
Cg, *Carapa guianensis*	(1, 2, 3)	Heliophilic (p)
Sm, *Sclerolobium melinonii*	(1, 2)	Heliophilic (p)
Dg, *Dicorynia guianensis*	(1)	Hemitolerant
Pv, *Peltogyne venosa*	(1)	Hemitolerant
Ef, *Eperua falcata*	(1)	Hemitolerant

Fig. 6 Relationship between wood cellulose $\delta^{13}C$ and bulk leaf $\delta^{13}C$ in trees of the different species growing in the forest and in a nearby 10-year-old plantation with monospecific plots. Data points represent average species values (±SE). The regression line corresponds to the pooled forest and plantation data sets. *Numbers* (1–3) represent the different groups of species distinguished by a cluster analysis based on both the leaf and wood cellulose $\delta^{13}C$ values of the trees growing in the forest. Average $\delta^{13}C$ values for the three clusters were:

Cluster 1: leaf $\delta^{13}C = -27.4‰ \pm 0.2$ SE, $\delta^{13}C$ of wood cellulose $= -25.4‰ \pm 0.3$SE.
Cluster 2: leaf $\delta^{13}C = -29.7‰ \pm 0.1$ SE, $\delta^{13}C$ of wood cellulose $= -26.3‰ \pm 0.5$ SE
Cluster 3: leaf $\delta^{13}C = -31.3‰ \pm 0.1$ SE, $\delta^{13}C$ of wood cellulose $= -27.6‰ \pm 0.4$ SE

The light adaptation features of the different species are those defined by Favrichon (1994) on the basis of growth observations made on established trees in the pristine cover or in response to microclimatic changes induced by thinnings with various intensities. Letter (*p*) refers to heliophilic pioneer or gap species

1982; Lesack and Melack 1996), direct measurements of the various nitrogen losses, and of the isotopic compositions of the different nitrogen sources of trees, are needed to substantiate such an hypothesis.

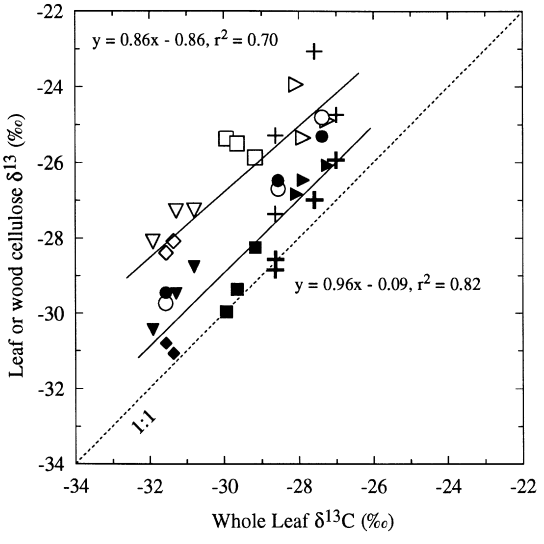


Fig. 7 Relationship between wood, or leaf, cellulose $\delta^{13}C$ and bulk leaf $\delta^{13}C$ in individual trees of different species growing in the forest and selected for their constrasting leaf $\delta^{13}C$ values (see Fig. 5). *Regression lines* between $\delta^{13}C$ of leaf cellulose and bulk leaf $\delta^{13}C$ and between $\delta^{13}C$ of wood cellulose and bulk leaf $\delta^{13}C$ are shown in the figure

Symbiotic associations and nitrogen acquisition types

Even though soil $\delta^{15}N$ values measured under the trees of different species in the forest were quite uniform (Fig. 4), leaf $\delta^{15}N$ values (Figs. 2, 4) as well as the difference $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ (Table 4) were highly variable among the species we investigated. Such interspecific differences are likely to be associated with differing N acquisition and utilisation features (Handley and Raven 1992).

Only three species, *Diplotropis purpurea*, *Recordoxylon speciosum* (Fabaceae), and *Sclerolobium melinonii* (Caesalpiniaceae), had root bacterial nodules (Table 1), and their presence was also associated with leaf N concentrations higher than 20 mg g^{-1} (Fig. 2). It is noteworthy that these three species only represented a very minor proportion (1.8%) of the stand basal area (Table 1). Högberg and Alexander (1995) found a similar percentage of nodulated species in a seasonally wet forest in Cameroon. Yoneyama et al. (1993) similarly found the contribution of root symbiotic N_2 fixation to be low in Amazonian forests of Brazil. The low proportion of fixing species may suggest that the forest we investigated is not nitrogen-limited, but primarily phosphorus-limited (Raaimakers et al. 1995), as is also suggested by the low leaf phosphorus concentrations we

Table 4 Difference in $\delta^{15}N$ (‰) between the surface soil (0–10 cm) and the leaves of the different species in the forest and in the plantation. Soil samples were taken under the trees on which leaves were sampled. For a given species, mean values (± SE) not sharing common letters are significantly different ($P < 0.05$). The presence of root nodules is denoted by the symbol *Nod*, the presence of root peritrophic associations is denoted by the symbol *Pta*

Species	Root symbiotic status	$\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ (‰)	
		Forest	Plantation
Dicorynia guianensis	Pta	0.79 ± 0.17	1.19 ± 0.59
Carapa guianensis		2.55 ± 0.39[a]	1.47 ± 0.11[b]
Eperua falcata	Pta	3.01 ± 0.30	2.28 ± 0.16
Sclerolobium melinonii	Nod, Pta	3.51 ± 0.14	nd
Goupia glabra		3.72 ± 0.18	3.54 ± 0.30
Diplotropis purpurea	Nod	4.46[c]	3.98 ± 0.10

[c] Single measurement

found (Table 2). However this hypothesis deserves further investigation since understorey legume species were not investigated in our study.

Although nodulated trees displayed significantly lower leaf $\delta^{15}N$ values than non-nodulated trees (Table 3), leaf $\delta^{15}N$ did not prove to be a straightforward indicator of symbiotic fixation: there was a clear overlap of $\delta^{15}N$ values for these two groups of species at the lower end of the $\delta^{15}N$ range (Fig. 2). Handley and Scrimgeour (1997) reached similar conclusions for species of a Scottish old field.

A group of nine non-nodulated species (see Fig. 2) displayed leaf $\delta^{15}N$ values that were within the range of the N_2-fixing species. It is noteworthy that the total leaf N concentrations of these species were lower than those in the N_2-fixing legumes (Fig. 2), which places them apart from this latter group. The following hypotheses may be put forward to explain the low leaf $\delta^{15}N$ in this group of species:

1. Rhizospheric N_2-fixation by free-living bacteria. Such processes have been reported to play an important role for nitrogen acquisition in grass dominated ecosystems (Balandreau 1976; Abbadie et al. 1992), but have not been studied in forest ecosystems to our knowledge.
2. Phyllospheric fixation by cyanobacteria (Freiberg 1994). This hypothesis is not contradictory to the rather low leaf N content found in the species of this group, because sampling was done during the dry season, while phyllospheric N_2-fixing cyanobacteria are active only during wet periods (Freiberg 1994).
3. The ability to use specific nitrogen sources with low $\delta^{15}N$ either biochemically (e.g. NH_4^+ instead of NO_3^-, Handley and Scrimgeour 1997) or spatially (architecture of root systems). Handley and Scrimgeour (1997) have stressed the importance of N-niche traits in the determination of plant $\delta^{15}N$ signatures.
4. The existence of nitrogen isotopic fractionations related to specific metabolic features (Handley and Raven 1992; Pate et al. 1993; Evans et al. 1996), or to symbiotic fungal associations (Högberg 1990; Handley and Raven 1992; Handley et al. 1993). In woodlands of Tasmania and Zambia, Högberg and Alexander (1995) found lower $\delta^{15}N$ values, which did not differ from the values of N_2-fixing species, in trees with vesicular-arbuscular (VA) endomycorrhizae than in ectomycorrhizal trees. Due to the absence of ectomycorrhizal fungi in the forest we studied (see also Béreau et al. 1997), such a relationship could not be tested. Whether different types of endomycorrhizae may lead to modulations in the leaf nitrogen isotopic signature remains to be investigated. Azcon et al. (1998) found that leaf $\delta^{15}N$ was altered by different endomycorrhizal fungal species for lettuce and barley. In our case the presence or absence of peritrophic associations did not influence $\delta^{15}N$, since the species displaying such structures (Table 1) varied greatly in their nitrogen isotopic signatures (Fig. 2).

Our results do not enable us to distinguish different trophic categories among the non-nodulated species with low $\delta^{15}N$, but constitute interesting starting points for future investigations. It would be particularly relevant to determine the nitrogen acquisition features for abundant species such as *Eperua falcata*, *Goupia glabra* or *Carapa guianensis* and to assess the possible role of these species in the nitrogen input in the ecosystem through fixation.

Leaf $\delta^{15}N$ values were clearly higher in the plantation than in the forest in the seven species common to both subsamples (see Fig. 2). However, the difference $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ significantly differed between the forest and the plantation in none of the species but *Carapa guianensis* (Table 4). Furthermore, leaf N concentrations were similar in the plantation and in the forest and the same ranking of species was observed for the difference $\delta^{15}N_{soil} - \delta^{15}N_{leaf}$ (Table 4) in both situations. The effects of perturbation on the different N acquisition patterns revealed by leaf $\delta^{15}N$ appeared to be limited in the 10-year-old plantation.

Interspecific diversity of carbon isotope discrimination

Considering the overall range of $\delta^{13}C$ variability obtained in this study, wood cellulose values were 2 to 3‰

higher than bulk leaf values both in the forest and in the plantation (Figs. 6, 7). To our knowledge our data present the first extension to the humid tropics of similar results that have largely been established in temperate trees displaying annual growth rings (Leavitt and Long 1982; Schleser 1990, 1992). In our case, only full sunlit leaves were sampled, whereas wood cellulose also integrated the contribution of shaded leaves that are more depleted in ^{13}C than sunlit leaves (van der Merwe and Medina 1989; Broadmeadow and Griffiths 1993; Buchmann et al. 1997a). Thus, the difference between bulk leaf $\delta^{13}C$ and wood cellulose $\delta^{13}C$ was an underestimate of the actual isotopic effect. Such an effect has primarily been attributed to differences in isotopic composition of the different plant biochemical compounds (Park and Epstein 1961). However, wood cellulose was also enriched in the heavier isotope as compared with leaf cellulose (Fig. 7), pointing to the existence of a specific isotopic fractionation for some metabolic step(s) in wood cellulose formation as suggested in *Juniperus monosperma* by Leavitt and Long (1982). Even though the precise nature of this latter effect remains unknown, it appears to be species-dependent since it was not found in *Carapa guianensis*, in contrast with the other species (Fig. 7).

In our study, leaf $\delta^{13}C$ values represented a time integration scale of less than a year, whereas wood cellulose values corresponded to several years of wood formation. Due to the absence of annual growth rings, this latter time scale could not be evaluated precisely. This difference in time integration scales reinforces the reliability of the differences in $\delta^{13}C$ among species we obtained, since results were consistent between the two types of measurements.

The present description of interspecific differences in leaf $\delta^{13}C$ (Fig. 5) is, to our knowledge, the first attempt to assess the overall variability of $\delta^{13}C$ values and to distinguish functional groups of species based on $\delta^{13}C$ in a tropical rainforest. The range of about 5‰ for average species $\delta^{13}C$ values we obtained, for sunlit leaves of species corresponding to a unique growth form (i.e. trees reaching the upper canopy layer, is clearly at the upper end of the ranges observed in other tropical, temperate or even boreal herbaceous (Körner et al. 1991) or forest (Balesdent et al. 1993; Marshall and Zhang 1994; Brooks et al. 1997) communities. According to the classical two-step model of carbon isotope discrimination during photosynthesis (Farquhar et al. 1982) and considering values of 360 μmol mol^{-1} and −8‰ for atmospheric CO_2 concentration and isotopic composition, respectively, the range of about 5‰ we observed between species for carbon isotope discrimination would correspond to a difference of 80 μmol mol^{-1} in average leaf airspace CO_2 concentration (C_i) and to intrinsic water-use efficiency (A/g) values ranging from 26 to 78 μmol mol^{-1}.

The important variability in $\delta^{13}C$ between – and within – species was not related to the variability in leaf $\delta^{15}N$, precluding one of the main hypotheses made at the beginning of this study (see introduction for potential underlying mechanisms). Furthermore, leaf $\delta^{13}C$ values were not related to N and P leaf concentrations both at the interspecific and intraspecific levels. It has been suggested (Lloyd et al. 1992; Epron et al. 1995) that, independently of leaf gas exchange regulation, interspecific differences in leaf $\delta^{13}C$ may be related to differences in leaf anatomical features determining the CO_2 diffusional conductance from the stomata to the chloroplasts. In our case, average leaf $\delta^{13}C$ values were independent of leaf thickness and of LMA, two variables that displayed considerable variation among species (Table 2). Thus, there was no evidence pointing to the role of leaf structure in determining $\delta^{13}C$.

We found an association, to some extent, between our cluster analysis based on $\delta^{13}C$ values in the different species (Fig. 6) and the one proposed by Favrichon (1994) who considered the plasticity of tree development with respect to light conditions (Table 1, Figs. 5, 6). Shade hemitolerant species presented the least negative $\delta^{13}C$ values (i.e. the highest intrinsic water-use efficiency). Pioneer and gap heliophilic species were included in a second cluster of species with more negative $\delta^{13}C$ values than in the former group (Figs. 5, 6), which is in accord with the observations made by Huc et al. (1994). A major and original result of the present study was to find a group of species (third cluster, Fig. 6), including very abundant species like *Eschweilera odora*, with $\delta^{13}C$ values even more negative than those of the pioneer and gap species. Surprisingly, this group emcompassed both heliophilic non pioneer species and late stage shade tolerant species (Favrichon 1994). Thus, the simple paradigms of pioneer/late stage or heliophilic/shade tolerant dichotomy (Huc et al. 1994; Condit et al. 1996) do not apply to describe interspecific differences in $\delta^{13}C$ in the tropical rainforest we studied.

The pattern of $\delta^{13}C$ distribution among species in the disturbed – and environmentally very different – conditions of the plantation was similar to the one observed in the forest, suggesting a predominant genetic control of this variable and thus of species average intercellular CO_2 concentration (Farquhar et al. 1989). Further studies on gas exchange regulation, hydraulic function, rooting and soil water extraction patterns are needed to refine the ecophysiological basis of the differential behaviour of tree species in tropical rainforests. The hypothesis that interspecific differences in $\delta^{13}C$ are associated with differences in water acquisition strategies, i.e. differences in rooting patterns and in the vertical gradients of water uptake by the roots, as it was suggested under Mediterranean conditions by Valentini et al. (1992) deserves particular attention. Some studies (Guehl 1984; Nepstad et al. 1994) have drawn attention to the role of deep water extraction in Amazonian forests. However, studies on differences among species in root architecture and vertical gradients of water acquisition remain scarce (Alexandre 1991).

In conclusion, our results show that single leaf $\delta^{15}N$ values cannot be used as a reliable indication of symbiotic N_2 fixation. However the dual isotope approach revealed considerable differences among species repre-

senting (1) widely differing intrinsic water-use efficiency, and (2) possibly the various N acquisition and utilisation types existing in an Amazonian rainforest. The absence of any relationship between $\delta^{13}C$ and $\delta^{15}N$ at the interspecific level, together with the lack of clear associations between the successional status, or shade tolerance, of the species and their isotopic signatures, are not in accord with the concept of the existence of functional types of species with common suites of traits underlying niche differentiation (Grime 1977; Tilman 1988). Our results, rather, support the hypothesis that each trait leads to a separate grouping of species. Further research directly addressing nitrogen, water and carbon acquisition and utilisation processes is needed for a thorough understanding of the role of biodiversity in the overall function of this type of ecosystem and its stability. The different species behaviours revealed by the nitrogen and carbon isotopic signatures were not altered by perturbations induced 10 years after the creation of monospecific even-aged covers. However, longer-term datasets are required for assessing the effects of such perturbations. Furthermore, the important variability of isotopic signatures observed in our study, suggests that any significant alteration in the floristic composition of the pristine cover may affect the overall nitrogen, carbon and water fluxes at the ecosystem level.

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